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Molluscan species diversity at North Pacific hydrothermal vents: What we know and what it may mean*

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Abstract: Hydrothermal vents in the deep sea are harsh, temporally unpredictable habitats with what appears to be a distinct fauna. Decades of subsea research with crewed and remote vehicles have generated a list of known species; is the species list complete? Evidence derived from mollusks sampled at hydrothermal vents on the East Pacific Rise (EPR), and Gorda and Juan de Fuca ridges suggests that the answer is yes. A 2006 compilation of hydrothermal vent species based on decades of research is updated and compared to specimens from these three active ridges in collections of the Field Museum of Natural History (FMNH) that resulted from limited collecting activity. Only three dives at each of the two Gorda Ridge vents collected all named species; 90% of the 20 species known from Juan de Fuca Ridge were collected in nine cruises. At the EPR, only 81% of the 43 known species were collected, but differences among the ridges were not significant. The limited FMNH collections increased the known ranges of six species from Juan de Fuca to Gorda Ridge and of nine species on the EPR. In addition, the EPR appears to host more rare species, potentially due to the frequent temporal changes at these vents. Mollusks currently known from each ridge, with their expanded ranges, are listed; the implications of these results for recent discoveries of slow-spreading vent fields are discussed.

Key words: Juan de Fuca Ridge; Gorda Ridge; East Pacific Rise; clam bed; collections

The deep sea, despite being the largest habitat on Earth, remains the least known. Since the discovery of seafloor hydrothermal vents on the East Pacific Rise, a large proportion of deep-sea research efforts have been devoted to these habitats. The rate of species description of the deep-sea hydrothermal vent fauna is unsurpassed. Has over 35 years of subsea and taxonomic research discovered all members of the vent fauna?

To address that question, I focus on the mollusk fauna of the East Pacific Rise (EPR) and the North East Pacific (NEP) Ridges of Juan de Fuca and Gorda. Mollusks offer an ideal group with which to address this question, as the phylum Mollusca comprises over 42% of the world's known vent fauna (Desbruyères *et al.* 2006); the Arthropoda and Annelida also form large percentages. The great depths at which vents lie, their distance from shore and the typically rocky terrain that surrounds them have limited prior collections of the vent fauna, meaning that few of the pertinent taxonomic groups had been discovered before the routine use of subsea vehicles. The onus of historical names that can create myriads of synonymies in more accessible faunas is thus avoided. Further, most vent mollusks from the North Pacific have been described by three experts (McLean 1988, 1989a, b, 1990, 1991, 1992, 1993, 2008, Warén and Bouchet 1986, 1989, 1993, 2001) who are uniquely familiar with the animals and who not only adhere to, but help establish, modern zoological standards. We can never answer the question of whether we know all species in a fauna, as one can never refute the existence of uncollected, undescribed species. However, the rate at which species are being described from these vents has declined and the list of known species is increasingly stable.

This paper documents the currently known molluscan species at hydrothermal vents on the East Pacific Rise (EPR) from 9° to 13°N and on the Gorda and Juan de Fuca Ridges (NEP). These areas are selected as they were the first hydrothermally active areas discovered, they have received considerable subsea research, and specimens from all three ridges are present in the collections of the Field Museum of Natural History. Are the mollusks that make up the hydrothermal vent fauna fully documented? How much collecting effort must be exerted to document the fauna at comparable, recently discovered vent fields?

The hydrothermal vent habitat

Hydrothermal vents release heat from deep within the Earth. As the heat warms the subsea crust, it initiates convection

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cells that draw seawater under the ocean floor. As the water transits the subsurface, it is heated and chemically reduced; oxygen is driven off and chemicals such as sulfates are reduced to sulfides. The hot, increasingly reduced fluid leaches metals from the sub-seafloor basalt and emerges supersaturated with metals. The metals precipitate, sometimes creating the illusion of smoke, when the hot fluid contacts the near 2° C seawater; large deposits of metal-rich sulfides can result (Van Dover 2000). Bacteria oxidize reduced chemicals to obtain energy; this energy in turn sustains the vent fauna. The existence of a bacteria-based ecosystem was unimagined before the discovery of hydrothermal vents in 1977 (Van Dover 2000).

Although the vent fluids contain energy-rich compounds that sustain microbial life, these same compounds can be toxic to animal life. High temperatures, low pH, high concentrations of dissolved heavy metals and deadly hydrogen sulfide in vent fluid may exclude non-specialized taxa from the vent habitat. In addition to its chemical rigors, the vent habitat is chronically unstable. Animal populations at vents can be affected by local and distant seismic events (Johnson *et al.* 2001); rock falls or events such as precipitation within a fluid conduit can alter or even stop fluid flow. Studies of fluid geochemistry have found that vent fluid salinity and often other characters change through the eruption cycle (Butterfield *et al.* 1997).

MATERIALS AND METHODS

The names and geographical ranges of molluscan species known from hydrothermal vents on the Gorda and Juan de Fuca Ridges (NEP) and the East Pacific Rise (EPR) reported by Desbruyères *et al.* (2006) were compiled; species descriptions or reports published more recently were added and are indicated in upper case in Tables 1 and 2. The widely available volume edited by Desbruyères *et al.* (2006) encompasses page-long genus or species-level treatments of the world's known vent fauna; authors are the appropriate experts for each taxonomic group. Although several years old, the treatments reflect decades of collecting and include photographs, diagnostic characters, biological information and the collection localities or known geographic ranges of each species. Are the decades of collecting effort that built this resource necessary to document the molluscan species at hydrothermal vents?

To address that question, the appended lists of mollusk species from NEP and EPR vents (Tables 1, 2) were compared to the mollusks collected from 1997 to 2003 during Remotely Operated Vehicle or the Human Occupied Vehicle ALVIN dives to vents on the three ridges. The collections were made during three dives in 2003 and 2004 at each of two active sites on Gorda Ridge (and one collection from 1988), nine cruises to active sites on Juan de Fuca Ridge, and two three-week long cruises on the EPR. One EPR cruise focused on 9°N, an area rarely included in published accounts of the vent fauna (*e.g.*, Tunnicliffe and Fowler 1996, Desbruyères *et al.* 2006); some of the specimens from this cruise are not deposited at FMNH and were not included in this report. FMNH collections cover the EPR between 8°37′N, Stauromedusa Field (Voight 2006), and 13°N and the off-axis field, Caldera (Voight *et al.* 2004). The section of the EPR between 9 and 13°N has received the most subsea research, as gauged by the online ALVIN dive log (Woods Hole Oceanographic Institute 2012), and is the focal area for the EPR in this report.

The collections are deposited in the Field Museum of Natural History (FMNH), having been sorted and identified using species descriptions and other literature (with some material sent for expert verification). Solenogastres were not identified to species. Each lot has been entered into the online database of hydrothermal vent invertebrates (Field Museum of Natural History 2012).

The sampling effort required to fully document a fauna reflects the diversity of the fauna. If the FMNH collections, which result from comparative minor sampling effort, contain most, if not all, the mollusk species known after decades of research at these hydrothermal vents, these vent mollusks will be concluded to be well-documented. To test this statement, the number of mollusk species in all literature reports for each ridge was compared to the number of mollusk species in FMNH collections for that ridge. Assigning significance to differences in the number of taxa on each ridge remains somewhat problematic. If FMNH collections compare well with the list of known species, with at least 90% of the total number of mollusk species known, the fauna will be considered to have been well sampled in the years since the first biological cruise to the EPR in 1979, since the 1981 discovery of vents on Juan de Fuca Ridge and since the 1988 discovery of hydrothermal activity at Escanaba Trough, Gorda Ridge.

In addition, comparing FMNH records to published reports allows our knowledge of the fauna to be refined. New records of a species from beyond its published geographic range, *e.g.*, the presence of a species previously recorded only from 13°N at 9°N, constitutes a range extension. These are indicated by boldface in the appropriate table.

With so little known of background deep-sea species, distinguishing taxa closely associated with vents from accidental or opportunist taxa can be problematic. To minimize this, I exclude here species that are known to primarily occur in non-vent, non-chemosynthetic habitats. For example, octopuses of *Graneledone* Joubin, 1918 are routinely seen at clam beds at NEP vent fields (*e.g.*, Juniper *et al.*, 1992) but they range widely in the deep sea (Voight 2008) and are

Table 1. The 23 molluscan species known from hydrothermal vents on Gorda and Juan de Fuca Ridges are listed following Bouchet *et al.* (2005). Additions to the species ranges (reported following Desbruyères *et al.* 2006) are indicated for species in **Bold** with the range extension indicated after the taxonomic authority. UPPER CASE = addition to fauna. TLO = type locality only. Site abbreviations are: ET = Escanaba Trough, Gorda Ridge; GR-14 = Seacliff, Gorda Ridge; Axial = Axial Seamount, Juan de Fuca Ridge; ES = Endeavour Segment, Juan de Fuca Ridge; MV = Middle Valley, Juan de Fuca Ridge.

Family, taxon name, authority (new record)	Distribution from Desbruyères *et al.* (2006)
Gastropoda	
Neolepetopsidae, ***Neolepetopsis gordensis*** McLean, 1990. (GR-14, see also McLean 2008)	ET
Neolepetopsidae, *PARALEPETOPSIS TUNNICLIFFAE* McLean, 2008	MV, TLO
Fissurellidae, *CORNISEPTA VERENAE* McLean and Geiger, 1998	Axial, TLO
Pseudococculinidae, *AMPHIPLICA GORDENSIS* McLean, 1991. "from sulfide crust"	Gorda - ET
Pyropeltidae, *Pyropelta musaica* McLean and Haszprunar, 1987	Axial; whale fall (McLean 1992)
Lepetodrilidae, ***Clypeosectus curvus*** McLean, 1989b. (ET, GR-14)	JFR
Lepetodrilidae, *Lepetodrilus fucensis* McLean, 1988	JFR
Lepetodrilidae, *Lepetodrilus corrugatus* McLean, 1993	MV, TLO
Lepetodrilidae, *LEPETODRILUS GORDENSIS* Johnson *et al.*, 2006	Gorda
Sutilizonidae, *Sutilizona tunnicliffae* Warén and Bouchet, 2001	JFR - ES, TLO
Sutilizonidae, *Temnocinclis euripes* McLean, 1989b	JFR - ES
Neomphalidae, *Lacunoides vitreus* Warén and Bouchet, 2001	Axial, TLO
Neomphalidae, ***Melanodrymia brightae*** Warén and Bouchet, 1993. (ET)	JFR - ES
Peltospiridae, ***Depressigyra globulus*** Warén and Bouchet, 1989. (ET; GR-14)	JFR
Seguenzioidea (unassigned) *ADEUOMPHALUS TROCHANTER* Warén and Bouchet, 2001?	Co-Axial, TLO
Turbinidae, (Skeneinae) ***Fucaria striata*** Warén and Bouchet, 1993. (ET)	JFR - ES
Provannidae, ***Provanna variabilis*** Warén and Bouchet, 1986. (ET; GR-14)	JFR
Buccinidae, *BUCCINUM THERMOPHILUM* Harasewych and Kantor, 2002	JFR - ES, TLO?
Hyalogyrinidae, ***Hyalogyrina globularis*** Warén and Bouchet, 2001. (ET; MV)	JFR - ES
Bivalvia	
Vesicomyidae, ***Calyptogena starobogatovi*** Krylova and Sahling, 2006. (MV; Clam Bed)	Axial
Vesicomyidae, ***Calyptogena diagonalis*** Barry and Kochevar, 1999. (ET; MV)	Monterey Canyon
Vesicomyidae, ***Ectenagena extenta*** Krylova and Moskalev, 1996. (ET; MV)	Monterey Canyon
Solenogasters	
Simrothiellidae, *Helicoradomenia juani* Scheltema and Kuzirian, 1991	JFR; Gorda
Six species known only from one site; only from holotype unless otherwise noted.	
Neolepetopsidae, *Paralepetopsis tunnicliffae* McLean, 2008	MV One or two specimens
Fissurellidae, *Cornisepta verenae* McLean and Geiger, 1998	AXIAL Holotype; Tunnicliffe (2012) shows 3 specimens
Lepetodrilidae, *Lepetodrilus corrugatus* McLean, 1993	MV Holotype
Neomphalidae, *Lacunoides vitreus* Warén and Bouchet, 2001	AXIAL 1 collection of 11 specimens
Sutilizonidae, *Sutilizona tunnicliffae* Warén and Bouchet, 2001	Endeavour 2 specimens (Geiger 2012)
Seguenzioidea (unassigned) *Adeuomphalus trochanter* Warén and Bouchet, 2001	Co-AXIAL (2 specimens in running shoe caught in grab)

excluded. Species found at organic falls and vents (*e.g.*, *Amphiplica gordensis* McLean, 1991; *Pyropelta musaica* McLean and Haszprunar, 1987) are included as members of the vent fauna, as are those also known from cold seeps (*e.g.*, vesicomyids *Ectenagena extenta* Krylova and Moskalev, 1996; *Calyptogena diagonalis* Barry and Kochevar, 1999). In their description of *Adeuomphalus trochanter,* Warén and Bouchet (2001) noted that the two known specimens were collected from a running shoe recovered with a grab near a vent on Juan de Fuca Ridge; Kano *et al.* (2009) question whether other members of the genus (often associated with sponges) are vent-dependent. I include this species in the list with a question mark.

Table 2. The 43 molluscan species known from hydrothermal vents on the East Pacific Rise between 9° and 21°N are listed following Bouchet *et al.* (2005), with three yet to be described and eight species known only from inactive areas. Additions to the species ranges (reported following Desbruyères *et al.* 2006) are indicated for species in **Bold** with the range extension indicated after the taxonomic authority. UPPER CASE = addition to fauna. Gal = Galapagos. TLO = type locality only.

Family, taxon name, authority (updated distribution)	Distribution from Desbruyères *et al.* (2006)
Gastropoda	
Neolepetopsidae, *Eulepetopsis vitrea* McLean, 1990	21°N–17°S
Lepetodrilidae, ***Clypeosectus delectus*** McLean, 1989a (9°N; 11°25′N)	13°N; 21°N
Lepetodrilidae, ***Gorgoleptis patulus*** McLean, 1988 (9°N)	13°N; Gal
Lepetodrilidae, ***Gorgoleptis spiralis*** McLean, 1988 (9N; 11°25′N)	13°N
Lepetodrilidae, *Gorgoleptis emarginatus* McLean, 1988	9°–21°N
Lepetodrilidae, ***Lepetodrilus cristatus*** McLean, 1988 (9°N)	13°N; 21°N
Lepetodrilidae, *Lepetodrilus elevatus* McLean, 1988	21°N–17°S
Lepetodrilidae, *Lepetodrilus pustulosus* McLean, 1988	21°N–17°S
Lepetodrilidae, *Lepetodrilus ovalis* McLean, 1988	21°N–17°S
Lepetodrilidae, *Lepetodrilus galriftensis* McLean, 1988	9°N; Gal
Lepetodrilidae, *Lepetodrilus tevnianus* McLean, 1993 (see Johnson *et al.* 2008; Bayer *et al.* 2011)	11°N
Sutilizonidae, *Temnozaga parilis* McLean, 1989a	21°–13°N
Neomphalidae, *Cyathermia naticoides* Warén and Bouchet, 1989	9°–21°N
Neomphalidae, *Melanodrymia aurantiaca* Hickman, 1984	21°N–17°S
Neomphalidae, *Melanodrymia galeronae* Warén and Bouchet, 2001	13°N, TLO
Neomphalidae, *Neomphalus fretterae* McLean, 1981	9°–21°N
Neomphalidae, *Pachydermia laevis* Warén and Bouchet, 1989	21°N–17°S
Neomphalidae, *Planorbidella planispira* Warén and Bouchet, 1989	21°N–17°S
Neomphalidae, *Solutigyra reticulata* Warén and Bouchet, 1989	13°N; 21°N
Peltospiridae, ***Ctenopelta porifera*** Warén and Bouchet, 1993 (9°N)	13°N
Peltospiridae, *Echinopelta fistulosa* McLean, 1989a	13°N; 21°N
Peltospiridae, *Hirtopelta hirta* McLean, 1989a	13°–21°N
Peltospiridae, *Lirapex granularis* Warén and Bouchet, 1989	9°–21°N
Peltospiridae, *Lirapex humata* Warén and Bouchet, 1989	21°N, TLO
Peltospiridae, ***Nodopelta heminoda*** McLean, 1989a (9°N)	13°; 21°N
Peltospiridae, ***Nodopelta rigneae*** Warén and Bouchet, 2001 (9°N)	13°N
Peltospiridae, ***Nodopelta subnoda*** McLean, 1989a (9°N)	13°N
Peltospiridae, *Peltospira delicata* Warén and Bouchet, 1989	9°–13°N
Peltospiridae, *Peltospira lamellifera* Warén and Bouchet, 1989	13°N, TLO
Peltospiridae, *Peltospira operculata* McLean, 1989a	9°–21°N; 17°S
Peltospiridae, *Rhyncopelta concentrica* McLean, 1989a	21°N–17°S
Chilodontidae, ***Bathymargarites symplector*** Warén and Bouchet, 1989 (9°N)	13°N; 21°N
Provannidae, *Provanna ios* Warén and Bouchet, 1986 (9°N; 11°25′N)	17°S; 13°–21°N
Provannidae, *Provanna muricata* Warén and Bouchet, 1986	21°N; Gal
Conidae, *Phymorhynchis major* Warén and Bouchet, 2001	13°–9°N
Bivalvia *n* = 3	
Vesicomyidae, *Calyptogena magnifica* Boss and Turner, 1980	21°N–23°S
Mytilidae, *Bathymodiolus thermophilus* Kenk and Wilson, 1985	13°N–21°S
Pectinidae, *Bathypecten vulcani* Schein-Fatton, 1985	9°–13°N
Solenogastres *n* = 4	
Simrothiellidae, *Sensilloherpia pholidota* Salvini-Plowen, 2008	13°N, TLO
Simrothiellidae, *Diptyaloherpia insolita* Salvini-Plowen, 2008	13°N, TLO
Simrothiellidae, *Helicoradomenia acredema* Scheltema, 2000	21°N; Gal; 17°S
Simrothiellidae, *Helicoradomenia bisquama* Scheltema, 2000	21°N, TLO

Table 2. (Continued)

Family, taxon name, authority (updated distribution)	Distribution from Desbruyères *et al.* (2006)
Cephalopoda *n* = 1	
Octopodidae, *Muusoctopus hydrothermalis* (González and Guerra, 1998) (9°N, 13°N; 11°25′N sight record)	13°N; 23°S
To be described	
Lepetodrilidae, *Lepetodrilus* aff. *galriftensis* McLean, 1988 see Johnson *et al.* (2008)	
Seguenzioidea (unassigned family) *Moelleriopsis* sp. Bush, 1897; Warén and Bouchet 1989	
Conidae, *Gymnobela* sp. A. Warén and Bouchet, 2001	13°–9°N
Eight species from inactive areas or vent margins; data from species descriptions	
Neolepetopsidae, *Neolepetopsis verruca* McLean, 1990	Inactive chimney at 21°N
Neolepetopsidae, *Neolepetopsis occulta* McLean, 1990	Sulfide at Green Seamount 21°N
Neolepetopsidae, *Neolepetopsis densata* McLean, 1990	Inactive chimney at 13°N
Fissurellidae, *CLATHROSEPTA DEPRESSA* McLean and Geiger, 1998	Volcano 5, 1160 m depth near 13°N, TLO
Fissurellidae, *CORNISEPTA LEVINAE* McLean and Geiger, 1998	Summit volcano 6, 1775 m depth near 13°N.TLO
Sutilizonidae, *Sutilizona theca* Warén and Bouchet, 2001	Inactive sulfides, *n* = 3, 13°N
Anatomidae, *ANATOMA JANETAE* Geiger, 2006	Caldera, 13°N; 8° 37′N
Anatomidae, *ANATOMA BATHYPACIFICA* (Geiger and McLean, 2010)	13°N, TLO (with anemones and serpulids)

Because the rate of species description is predicted to slow as a fauna becomes better known, rate changes can indicate our knowledge of the fauna. The publication dates for all mollusk species from each of the three ridges were compiled and the median calculated. In addition, the number of species described in 2000 (or since) were totaled for each ridge. A pulse of recent species descriptions would indicate recent discovery, with all things (such as delays in preparing the description) being equal.

Rare and/or narrowly endemic species could indicate insufficient sampling, areas of high endemism, or they could indicate suspect inclusions which limit our knowledge of true diversity (Thessen *et al.* 2012). Thus, species which available data indicate occur at only one site and those known only from the type series merit special attention. To consider whether high endemicity at a site might relate to other factors, the site's depth and basic geology were considered. In addition, changes in vent fluid chemistry over the eruption cycle could affect faunal composition. To consider whether the collection of rare species relates to the timing of rare events, such as eruptions, I relied on literature accounts (Johnson *et al.* 2008, Bayer *et al.* 2011) that, although they do not report the deposition of voucher specimens, include specimen photos and cite singular events.

To document how molluscan species diversity compares among different vent fields on a ridge, the number of different species recorded from each vent field that was sampled at least nine times was compared. All samples, from push cores to grab samples of tube worm clusters with all associated fauna, were included. Including only fields that are represented by at least nine samples attempts to assure comparable sampling effort. Within Juan de Fuca, the total number of species collected from Endeavour Segment, a large complex area (Kelly *et al.* 2012), was determined. All samples from a ridge were pooled to determine the total sampling effort for that ridge and the total number of molluscan species collected from that ridge.

RESULTS

Table 1 lists 23 mollusks including 19 gastropods, three bivalves, and a solenogastre known from hydrothermal vents on Gorda and Juan de Fuca Ridges in the Northeast Pacific. Eight species have been added to those species listed for Juan de Fuca and Gorda Ridges by Desbruyères *et al.* (2006), including 3 species described in or after 2006. Two vesicomyid species described from cold seeps near Monterey Canyon are recorded on both ridges. Gorda Ridge hosts 12 known species, including two vesicomyids. FMNH records extend the known ranges of six species known from Juan de Fuca to Gorda Ridge (Table 1). In total, 10 or 43.5% of all species range more widely than reported in Desbruyères *et al.* (2006).

Juan de Fuca Ridge is home to 20 known molluscan species, including two described from FMNH collections. Hydrothermal vents on Axial Volcano host three species that are not known to occur elsewhere on the ridge. Only the type

collections of two (*Cornisepta verenae* McLean and Geiger, 1998; *Lacunoides vitreus* Warén and Bouchet, 2001) are known (Table 1); the third species, *Pyropelta musaica*, is also known from whale falls (McLean 1992). Middle Valley, Juan de Fuca Ridge, a sedimented hydrothermal field, has the highest known molluscan species diversity of these vent fields with widely distributed Juan de Fuca Ridge species and two (*Lepetodrilus corrugatus* McLean, 1993; *Paralepetopsis tunnicliffae* McLean, 2008) known only from one or two specimens (Table 1). Clam Bed on Endeavour Segment has 12 species.

The description of the limpet, *Lepetodrilus gordensis* Johnson, Young, Jones, Warén and Vrijenhoek, 2006, documents it to be endemic to Gorda Ridge; although the species has been collected from Juan de Fuca Ridge, this collection was concluded to be contamination (Voight *et al.* 2012). *Amphiplica gordensis*, described from a sulfide crust at Escanaba Trough, has been reported from GR-14 by Clague *et al.* (2001) and genetically identical specimens have been collected from wood and whale falls (Kano *et al.* 2013). Clague *et al.* (2001) also report *Provanna laevis* Warén and Ponder, 1991, described from Guaymas vents in the Gulf of California and present at North Pacific cold seeps (Sahling *et al.* 2002), from GR-14. Given the difficulties in distinguishing North Pacific species in *Provanna* Dall, 1918 (A. Warén, pers. comm.), I choose to leave this question unresolved.

Table 2 lists the 43 mollusk species known from EPR vents from 9° to 21°N, with what may be three additional vent-associated species as yet unnamed. In addition are the eight species (Table 2) described from either inactive areas such as extinct sulfides or from near vents but among what appear to be typically background fauna, *i.e.*, *Anatoma bathypacifica* (Geiger and McLean, 2010) and *A. janetae* Geiger, 2006. I do not discuss these in detail. FMNH collections, most notably from vents near 9°N and Flo and Bucky at 11.415°N, expand the known distribution of nine species (Table 2) that had been known only from 13°N. The range of nearly 21% of the species is expanded here compared to that reported in Desbruyères *et al.* (2006). Two species, (*Provanna ios* Warén and Bouchet, 1986; *Muusoctopus hydrothermalis* (González and Guerra, in González *et al.*, 1998)) that had been known only from sites far to the south and to the north, were recorded from 9°N. Their distributions are likely more continuous than has been documented.

Three gastropod species described from EPR vents, *Melanodrymia galeronae* Warén and Bouchet, 2001, *Lirapex humata* Warén and Bouchet, 2001, and *Peltospira lamellifera* Warén and Bouchet, 1989, remain known only from their type localities, all either at 13° or 21°N. These and three solenogastres known only from their type locality composed nearly 14% of the mollusk fauna. As *Provanna muricata* Warén and Bouchet, 1986 has been collected from 21°N and from near the equator at the Galapagos vents (Desbruyères *et al.* 2006), it would seem likely to also occur between 9° and 13°N. *Lepetodrilus tevnianus* McLean, 1993 has been reported in the taxonomic literature only from near 11°N (Warén *et al.* 2006), but as discussed below, Johnson *et al.* (2008) and Bayer *et al.* (2011) report that it occurs more broadly.

The median years of species description, 1989 for the EPR and 1993 for both Juan de Fuca and Gorda Ridges, are not significantly different. Neither do the number of species descriptions published in or since 2000 differ among the ridges (Gorda, 1; Juan de Fuca, 7; EPR 9; G-test; $G = 1.988$).

FMNH collections hold all molluscan species known to occur on Gorda Ridge, despite having specimens from just three dives to each of the two known vent fields. Of the 20 mollusk species known to occur on Juan de Fuca Ridge, 90% were collected in 9 cruises involving FMNH. Only 35 of the 43 known mollusks (81%) from EPR vents are present in FMNH collections made during two three-week long cruises, although not all the material collected during these cruises was deposited at FMNH. However, no significant difference in the proportion of known species that were collected exists among the three ridges (G-test; $G = 0.1895$, $df = 5$).

Ridge membership appears strongly associated with species diversity; the EPR has the most (45) molluscan species and Gorda Ridge has the least (12). Within a ridge, more sampling at a vent field usually increases the total species collected (Table 3). Exceptionally, more species were documented in fewer samples from Clam Bed on Juan de Fuca Ridge than from Main Field Endeavour. The presence of a clam bed habitat may increase the total species.

DISCUSSION

Collections at FMNH hold 100% of the mollusks known from Gorda Ridge, and 90% and 85% of those known from Juan de Fuca Ridge and the East Pacific Rise, respectively. The high proportion of the known species collected from active vents during two cruises to Gorda Ridge, nine to Juan de Fuca Ridge and two to the EPR suggest that this limited collecting effort effectively sampled the mollusks known at these hydrothermal vents. The molluscan species level diversity at these active ridges is well known.

These collections also resulted in specimens that served as the basis for the descriptions of two vent-associated species in the NEP (*Hyalogyrina globularis* Warén and Bouchet, 2001, *Lacunoides vitreus*) and two species collected with non-vent fauna on the EPR (*Anatoma janetae*, *A. bathypacifica*). Does the description of 10% of the Northeast Pacific molluscan vent species from these collections contradict this statement? Specimens of *H. globularis* had been collected as early as 1988 (FMNH 309720). Its discovery was likely delayed by its overall similarity to the peltospirid, *Depressigyra globulus* Warén

Table 3. The number of discrete sampling events and the cumulative number of species in FMNH collections from each ridge, by site and pooled.

	Sampling Events	Mollusk spp. Collected	Spp. Known from Ridge
Gorda Ridge			
Escanaba Trough	21	12*	
GR-14 (Seacliff)	9	6	
Total Gorda Ridge	**30**	**12***	**12**
Juan de Fuca Ridge			
Main Field Endeavour	10	8	
Clam Bed	9	12*	
Endeavour Segment (Main Field Endeavour, Clam Bed, Raven, Quebec, Beach, Axial)	40	16*	
Total Juan de Fuca Ridge (Endeavour Segment above plus Middle Valley)	**44**	**18* (90%)**	**20**
East Pacific Rise			
9°N	26	29*	
13°N	19	20	
Caldera (slightly off-axis)	23	19	
13°N + Caldera	42	30	
Total East Pacific Rise (Stauromedusa Field (8°37′N); 9°N; Flo and Bucky (11°25′N); 13°N; Caldera)	**80**	**35* (81%)**	**43**

* Indicates a clam bed was sampled.

and Bouchet, 1989. The species *L. vitreus*, discussed further below, may represent one of the vanishingly rare species that may exist undetected in most habitats.

At both NEP and EPR vents, six species are known only from their type localities. Given that more species occur on the EPR, in terms of percent, this is nearly twice as many. Nine species from each area are also identified as having range extensions, percentage-wise, nearly twice as many at NEP vents than at EPR vents. Does this indicate the northern fauna is less well known? I suspect that the difference in range extensions reflects the uneven research effort at Juan de Fuca and Gorda Ridges. Gorda is notorious for poor weather; it has been subject to less research than has the more northern ridge. Whether the different frequencies of species known only from their type localities are biologically meaningful, I leave open to discussion, while noting that nearly half of those at EPR in this category are solenogastres, which are rarely identified to species, while those at NEP are all gastropods.

The harsh, temporally dynamic and stochastically distributed vent habitat is often dominated by one or very few species. The perpetual problem in determining the true species diversity at vents can be locating rare taxa among the hyper-abundant ones. For example, Juniper *et al.* (1992) report three gastropods, *Lepetodrilus fucensis* McLean, 1988, *Depressigyra globulus*, and *Provanna variabilis* Warén and Bouchet, 1986 and two polychaetes, *Ridgeia piscesae* and *Amphisamytha galapagensis*, to comprise over 73% of all animals in 8 samples from Middle Valley, a vent with high molluscan diversity. Northeast Pacific limpets of *L. fucensis* and *L. gordensis* host bacteria on their gills (Bates 2007). Perhaps reliance on symbiotic bacteria frees the limpets from competition for food; they can live in stacks and reach extraordinary densities (> 100,000 m^{-2}; Bates 2007).

Not included here with the vent fauna are species from inactive sulfides (Table 2), most of which are known only from their type localities, or only from the holotype. These areas of previous hydrothermal activity are the target of proposed subsea mining, yet are among the least known vent-associated habitats. Whether these species are obligate associates of this habitat, how common they are, how they feed, and whether they exploit a special niche created by these habitats remain unanswered questions.

Two sites, Axial Volcano and Middle Valley appear to have unusually high numbers of endemic species (Table 1). On the Mid-Atlantic Ridge, the fauna of the two shallowest vent fields, Lucky Strike and Menez Gwen, is slightly more diverse than that of the deeper vent fields; depth may be a causal factor in this difference (Van Dover *et al.* 1996, Van Dover 2000). Depth may also contribute to the presence of unique species at Axial, the shallowest vent field on Juan de Fuca Ridge. Middle Valley is unusual in being sediment covered, as is Escanaba Trough on Gorda Ridge. These two vent fields, separated by 2500 km, share two species, *Ectenagena*

extenta and *Solemya* Lamarck, 1818 sp. (represented only by shell fragments from the hydrocarbon seep) that are otherwise unknown from Northeast Pacific Ridges. At a hydrothermally modified hydrocarbon seep at Escanaba Trough on Gorda Ridge, the bivalves *Ectenagena extenta*, *Solemya* sp. and *Calyptogena diagonalis* Barry and Kochevar, 1999 use hydrocarbons for energy, but they can only be sustained due to hydrothermal input (Kvenvolden *et al.* 1986, Clague *et al.* 2001).

Differences in ridge spreading rate appear to be linked to differences in ridge species diversity (Van Dover 2000). EPR has the fastest spreading rate, which has been linked to smaller, less stable vents, and higher species diversity. At EPR vents, phases of faunal succession characterize the initiation and denouement of hydrothermal activity. Tube worms of *Tevnia* typically colonize newly active vent sites, to be succeeded by tube worms of *Riftia*, which in time are replaced by mussels of *Bathymodiolus thermophilus* Kenk and Wilson, 1985 (Hessler *et al.* 1988, Mullineaux *et al.* 2000). Comparable successional changes likely also affect smaller taxa. One example may be *Lepetodrilus tevnianus*, a species so rare in collections that Warén *et al.* (2006) considered it to be known only from its type locality at 11°N. However, Bayer *et al.* (2011) consider it and *Ctenopelta porifera* Warén and Bouchet, 1993, to be "pioneer" species. They collected over 2600 individuals at post-eruption vents at 9°N; Johnson *et al.* (2008) also report it from 9°N to 7°S.

A comparable sequence of faunal change at NEP vents is as yet unknown (Tsumuri and Tunnicliffe 2001, Marcus *et al.* 2009), but *Lacunoides vitreus*, to my knowledge collected only once, may be an example. The 11 specimens were collected 6 months before the 1998 eruption of Axial Volcano in the midst of a massive new settlement of the vent gastropod species. Resolving what species remain undiscovered at hydrothermal vents requires that collections be made throughout the eruption cycle. Although unpredictable, the cycle is likely much longer on slow spreading than on fast-spreading ridges. Even on the best-studied ridges, currently unknown taxa may characterize some stages, despite the significant effort that has already been expended.

At EPR vents, a snapshot view of the fauna would show that gastropods partition habitats to a much greater extent than they do on NEP vents. The hot smoker habitat supports species of *Nodopelta* McLean, 1989a and the tube worm habitat supports species of *Lepetodrilus* McLean, 1988; at NEP vents, the smoker habitats are largely mollusk-free and *L. fucensis* or *L. gordensis, Provanna variabilis* and *Depressigyra globulus* partition the remaining habitat by temperature (Bates *et al.* 2005).

The existence of cryptic species, or species complexes, is still being unraveled among the vent fauna (*e.g.*, Stiller *et al.* 2013). Their presence cannot be refuted among the vent mollusks. Johnson *et al.* (2006) used gene sequences to distinguish *L. fucensis* from *L. gordensis* and supported the genetic difference with morphological differences. Although this discovery could be cited to argue that the formerly contiguous Gorda and Juan de Fuca faunas have begun to diverge to a greater extent than Table 1 indicates, these *Lepetodrilus* spp. may be exceptional. Both *L. fucensis* and *L. gordensis* rely on symbiotic bacteria that are thought to oxidize sulfide in the vent fluids for food (Bates 2007). Differences in the concentration of sulfide in the vent fluids of the two ridges, with that of Gorda being more limited (Von Damm *et al.* 2005, 2006), may have accelerated divergence of these species (Beinart *et al.* 2012).

Implications for the future

Ridge spreading rate has been associated with the size and stability of vent fields and the number of active vents, with slow spreading ridges having few, large and stable vents (Baker and Hammond 1992, but see Baker and German 2004 for a different view). If the slow spreading rate of Gorda Ridge is linked to its low species diversity, it bodes well for current research. Recently discovered vents in the first phases of exploration lie on slow-spreading ridges, such as those in the Indian Ocean, the Arctic and the Cayman Trough (Connelly *et al.* 2012, Nakamura *et al.* 2012, Rogers *et al.* 2012, Tao *et al.* 2012). Time-tested collection methods may efficiently and rapidly document most of the fauna of vents on these slow-spreading ridges.

The most recent reports of new vents also report the discovery of new species, but do not name the new species. The basis of those statements is that the COI gene sequence of these new species differs sufficiently from that known for other, previously named congeneric taxa (Connelly *et al.* 2012, Nakamura *et al.* 2012, Rogers *et al.* 2012, Tao *et al.* 2012). Whether such analyses represent the new minimum for species determination will depend on whether specimens of the new taxa are shared with expert taxonomists. Experts who describe species not only identify how species differ and assign names, they provide fundamental information on morphology and anatomy. These collections can be used to build robust phylogenies that will allow us to understand not just species, but their evolution and the history of hydrothermal vents.

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